



Original article

Current and potential future distribution of the American dog tick (*Dermacentor variabilis*, Say) in North America

Jordan N. Minigan^a, Heather A. Hager^a, Andrew S. Peregrine^b, Jonathan A. Newman^{a,*}

^a Department of Integrative Biology, University of Guelph, Canada

^b Department of Pathobiology, University of Guelph, Canada



ARTICLE INFO

Keywords:

Climate change

Dermacentor variabilis

Species distribution model

ABSTRACT

The American dog tick (*Dermacentor variabilis*) is medically and economically important in North America. This species is found across central and eastern North America from the Gulf Coast of Mexico through southern Canada. In parts of this region, *D. variabilis* is a vector for pathogens that cause diseases in humans and animals. Our aim was to determine whether climate change would affect the distribution of the climatically suitable area for *D. variabilis* in North America, to aid monitoring for potential future spread of tick-borne pathogens. We developed a species distribution model for *D. variabilis* to project where climate will likely be suitable for the tick in North America using a maximum entropy method, occurrence records from museum and laboratory archives, and 10 environmental variables relevant to climate requirements for the tick. We used four emissions scenarios from the Intergovernmental Panel on Climate Change's Fifth Assessment Report and 10 climate models from the Coupled Model Intercomparison Project (phase 5) to estimate potential future climate suitability and determine how the tick's distribution could change. Our consensus model projected that the area of suitable climate in North America could increase from present by approximately 50% by 2070. In areas beyond the current northern limit of *D. variabilis*, climate could become more suitable for the tick than at present, possibly resulting in a northward expansion in Canada, but the potential suitability of the southern range of *D. variabilis* could decrease, depending on the region and climate model. Due to the ability of *D. variabilis* to harbor and transmit pathogens, a change in the distribution of this species could also affect the risk of human and animal diseases throughout North America, particularly in the northern range of the tick.

1. Introduction

Globally, ticks are among the most important vectors of human and animal pathogens (Jongejan and Uilenberg, 2004; Troughton and Levin, 2007; Thomas and Beierkuhnlein, 2013). Ticks are second only to mosquitoes with respect to overall impact as vector species, but they harbor and transmit a wider variety of pathogens than all other arthropods (Sonenshine, 1991). Further, the number of known tick-borne pathogens has increased since the 1980s (Fayer, 2000). In conjunction with changing tick population dynamics and increased exposure of humans and animals to ticks, this has resulted in the emergence of tick-borne diseases as more serious global human and animal health concerns than ever before (Pfäffle et al., 2013).

It has been suggested that climate change is likely to be the primary driver of many aspects of tick-borne pathogen transmission, particularly the changing population dynamics of tick species (Fayer, 2000; Kocan et al., 2010). Climate change can influence tick vectors directly by altering phenology and overall survival. It can also affect tick vectors

indirectly through changes to habitat availability, host abundance, and host distribution. In turn, these changes influence the tick-pathogen relationship through changes in the availability of host species that serve as reservoirs for tick-borne pathogens (Jongejan and Uilenberg, 2004). The combination of potential changes to tick populations, host populations, and host-pathogen interactions ultimately influence the likelihood of tick-borne pathogen transmission to human and animal populations (Brownstein et al., 2005; Pfäffle et al., 2013). Accordingly, an understanding of the future risk of tick-borne diseases begins with an investigation of the effects of climate change on the tick vector, in addition to host species and habitat suitability, as well as the effects of these changes on pathogen transmission (Gage et al., 2008). Here, we examine the effects of climate change.

Studies have shown that some tick vectors have experienced, or could experience, range shifts under climate change (Léger et al., 2013). In Europe, the castor bean tick (*Ixodes ricinus*) is a vector for pathogens that cause Lyme borreliosis (*Borrelia* spp.) and tick-borne encephalitis (tick-borne encephalitis virus) in humans. Porretta et al.

* Corresponding author.

E-mail address: jonathan.newman@uoguelph.ca (J.A. Newman).

(2013) projected that *I. ricinus* could disperse throughout a larger area of Europe than where it is currently found, and Lindgren and Gustafson (2001) observed an increase in disease incidence associated with increasing *I. ricinus* presence, which they argue was likely influenced by climate change. Similarly, the blacklegged tick (*Ixodes scapularis*), a vector of *Borrelia burgdorferi*, the causative agent of Lyme borreliosis in North America, has already dispersed north and west in Canada, playing a role in increasing Lyme borreliosis incidence (Bouchard et al., 2015). Under climate change, the distribution of *I. scapularis* will likely continue to expand throughout northeastern parts of North America (Brownstein et al., 2005; Ogden et al., 2006, 2008; Leighton et al., 2012). Other studies have found that the distribution of some ticks has not changed over time, such as that of *Dermacentor andersoni*, a vector for several human and animal pathogens that cause diseases such as Rocky Mountain spotted fever and tularemia (James et al., 2006; Dergousoff et al., 2013). This lack of change is potentially related to habitat availability for host species, rather than climate *per se* (James et al., 2006).

The American dog tick (*Dermacentor variabilis*) is a medically and economically important tick species in North America. It occurs in brushy field habitat and is currently widely distributed throughout the eastern United States from the Gulf of Mexico to New England, and through the Midwestern states. There is also an isolated population of *D. variabilis* along the West Coast of the United States, concentrated in California (Bishopp and Trembley, 1945; Eisen et al., 2006; Sonenshine, 1993; Pfäffle et al., 2013). In Mexico, *D. variabilis* can be found in states along the Gulf Coast (Guzmán-Cornejo et al., 2016). In Canada, *D. variabilis* is typically found in southern parts of Ontario, Manitoba, Saskatchewan, and throughout Nova Scotia. It has been suggested that *D. variabilis* has become increasingly prevalent over time in these provinces (Bishopp and Trembley, 1945; Dodds et al., 1969; Burg, 2001; Dergousoff et al., 2013). Throughout the distribution of the tick, the usual host species range from small mammals such as mice, voles, and raccoons to larger mammals such as dogs, cervids, and wild and domestic ruminants (Bishopp and Trembley, 1945; Sonenshine, 1991).

In parts of its distribution, *D. variabilis* is the primary vector of multiple pathogens that affect human and animal health, including *Francisella tularensis*, the cause of tularemia; and *Rickettsia* spp. bacteria, which cause spotted fevers (Jongejan and Uilenberg, 2004; Dergousoff et al., 2013). *D. variabilis* also transmits *Anaplasma marginale*, which causes bovine anaplasmosis (Kocan et al., 2010; Aubry and Geale, 2011). Currently, most of these tick-borne pathogens occur infrequently throughout the distribution of *D. variabilis*, particularly those affecting human health (Dergousoff et al., 2013). Some pathogens, such as *A. marginale* and *Rickettsia rickettsii* (the cause of Rocky Mountain spotted fever), appear to be absent from the Canadian portion of the distribution of *D. variabilis*, so bovine anaplasmosis and Rocky Mountain spotted fever do not occur in these regions, despite *D. variabilis* presence (Howden et al., 2010; Lysyk, 2013). However, based on the responses of other tick species and observations by Dergousoff et al. (2013), which suggest that northward expansion of the *D. variabilis* range is possible or already occurring, it is possible that tick-host and tick-pathogen encounters could occur more frequently due to increasing abundance, or in new areas due to range expansion. During a range expansion, tick populations establish in areas that are currently not inhabited by ticks, and they can introduce pathogens to areas where they are currently absent by feeding on uninfected hosts and causing infection. Increasing tick abundance or a range expansion can, therefore, result in an increased risk of tick-borne disease (Wimberly et al., 2008).

Awareness of disease risk is key in disease prevention strategies. Thus, it is important to first understand how risk of exposure to a vector species can change over time, and whether pathogen transmission is possible (Rand et al., 2007; Wimberly et al., 2008). Species distribution models have become popular tools for modeling the responses of individual species to climate change (Guisan and Zimmermann, 2000; Elith et al., 2011), including arthropods such as ticks (Ogden et al.,

2006; Leighton et al., 2012; Porretta et al., 2013). Species distribution models aim to represent the ecological niche of a species by locating geographic areas where the environmental conditions required for that species most likely occur. They can be used to model the past, present, and future distribution of a species and are able to include the effects of climate change (Martinez-Meyer, 2005; Elith and Leathwick, 2009). As discussed by Porter and Kearney (2009), it is impossible to include all components of a species' niche in a species distribution model because many of the components are often unknown. Furthermore, including all of them could produce an overly complex model. In the case of ticks, climate is often a primary limiting factor for the development and survival of the immature stages and is an important component of the niche to consider when distributional changes are of interest (Gage et al., 2008).

Three species distribution models have recently been developed for *D. variabilis*: Atkinson et al. (2012) modeled the distribution of *D. variabilis* in Texas, relating it to the spread of *R. rickettsii* in humans and dogs; St. John et al. (2016) modeled the distribution of *Rickettsia montanensis*-positive and -negative *D. variabilis* in the United States to improve the understanding of other spotted fever group bacteria; and James et al. (2015) modeled the current distribution of *D. variabilis* in the United States, with the goal of determining which environmental factors are the most important determinants of the distribution of the tick. Here, we aimed to (1) extend the model by James et al. (2015) to include the entirety of North America (Canada, United States, and Mexico), representing the complete current distribution of *D. variabilis*, and (2) apply future climate change scenarios to the model to investigate how the distribution of *D. variabilis* could change across the continent over the remainder of the current century.

2. Methods

We developed our species distribution model for *D. variabilis* using Maxent v3.3.3 (Phillips et al., 2006). Maxent is a form of logistic regression that uses presence-only data for model development, and often outperforms other presence-only modeling methods with respect to predictive accuracy (Phillips et al., 2006). Absence data are not included because these records are often unreliable and challenging to acquire, particularly when relying on passive surveillance data, as we have done here (Elith et al., 2006). All maps and geospatial analyses were completed using ArcGIS 10.3.1 (ESRI, 2014). All *D. variabilis* occurrence data and environmental data used for this modeling effort are archived at the University of Guelph Agri-Environmental Research Data Repository (Minigan et al., 2015).

2.1. Tick occurrence data

In total we used 3063 occurrence records in this model for *D. variabilis*. All records shared the same date range as the baseline environmental data (approximately 1950–2000s). Including occurrence data from a large date range may obscure recent changes in tick distribution, but when modeling the future, such as when making climate change projections, both occurrence and environmental data should share the same time frame (James et al., 2015). Records were not used if location identifiers or year of collection were unclear or ambiguous.

We obtained occurrence records for *D. variabilis* in the United States as the number of records per county from the United States Department of Agriculture National Veterinary Services Laboratory (Iowa, United States) and the United States Museum of Natural History National Tick Collection (Georgia Southern University, United States). We considered records that occurred within national or state parks to occur within the county that intersected the majority of the park area. To produce geographic coordinates for the occurrence points, we used ArcGIS to randomly distribute the same number of points as there were records in each county (as per Atkinson et al., 2012), under the assumption that climate conditions were likely to remain consistent at the county level.

We used the ‘Calculate Geometry’ tool in ArcGIS to obtain specific co-ordinates for each point and reduced the density of the occurrence points to one record within a 4 km radius to match the resolution of the climate data (outlined below) and to reduce spatial autocorrelation between the points.

We received Canadian occurrence data primarily from IDEXX Laboratories, Inc. (Canada) as the number of records per Forward Sortation Area (FSA) of postal codes corresponding with veterinary clinics that submitted ticks found on wildlife or pets. We produced geographic coordinates for the occurrence records in each FSA using the same method described above. Additional records of *D. variabilis* in Canada were obtained from Lindquist et al. (2016) and these data indicate the presence of the tick in cities and towns; geographic co-ordinates for these records represent the centroid of the city or town in which the ticks were located.

We obtained data outlining the distribution of *D. variabilis* in Mexico from Guzmán-Cornejo et al. (2016). These records represented the presence of *D. variabilis* at various localities (e.g. cities or municipalities) in Mexican states. Geographic coordinates for many of these records were provided by Guzmán-Cornejo et al. (2016), and we identified the coordinates for the remaining localities using Google Maps (Google Maps, 2017).

When using presence-only data from museum and laboratory archives, it is important to be aware that the data may be subject to biases related to the original sampling methods (Franklin, 2009; Phillips et al., 2009). First, sampling often occurs in locations that are reasonably accessible to researchers for collection, such as near roads or trails, and locations that are most accessible to the vertebrate hosts on which the ticks are found, such as rodents, raccoons, and dogs. The distribution of occurrence points may represent sampling effort rather than the geographic distribution of the species; however, collecting data from multiple sources, as we have done here, can reduce this bias (Pacifi et al., 2017). Second, the true location of origin may be uncertain if the tick was unknowingly transported from one location to another on humans or animals and found later. However, lacking a non-arbitrary means of identifying adventitious ticks, we assumed that the occurrence records accurately represented the location of origin of the tick. We believe this assumption is reasonably robust because climate occurs at a large scale relative to the boundaries within which we distributed occurrence points (i.e. counties, FSAs, and cities), so it is likely that records distributed near, but not at, their true location of origin will exhibit similar climate conditions to their true location of origin. Nevertheless, passive surveillance data are still likely to lead to some degree of overestimation in distributions; more accurate predictions could be made if field observations were readily available. Lastly, misidentified tick submissions can contribute incorrect occurrence records, particularly in areas where the ranges of species overlap. *D. andersoni*, the tick that morphologically is most similar to *D. variabilis*, is commonly found in western Canada and the United States; however, the ranges of *D. andersoni* and *D. variabilis* have only recently overlapped in Saskatchewan (Dergousoff et al., 2013), suggesting that these tick species do not commonly exist in the same parts of North America.

2.2. Environmental variables

We developed this model using environmental variables that are biologically relevant to *D. variabilis* (Araújo and Pearson, 2005) and could play a role in determining the distribution of the tick in North America. We downloaded altitude data and 19 bioclimatic variables related to temperature and precipitation means and ranges from Worldclim (<http://www.worldclim.org>; Hijmans et al., 2005) as geospatial data with a resolution of 2.5 arc minutes (approximately 4 km). All data layers were clipped to the boundaries of North America, re-sampled to ensure equal grid size and spatial extent, and projected to the North American Albers Equal Area projection.

To achieve the most parsimonious model for *D. variabilis*, we did not

Table 1
Variable combinations evaluated for use in development of the *D. variabilis* species distribution model with all North America (Canada, United States, and Mexico) occurrence data, and associated Akaike Information Criterion (AIC) values. The first row is the base model. The base model comprised all the variables used by James et al. (2015): July Normalized Difference Vegetation Index (NDVI), mean diurnal temperature range, isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of wettest month, precipitation seasonality. We did not include NDVI because there were no NDVI projections readily available for the future climate projections. The subsequent rows show the variables that were added to the base model and the resulting AIC.

Variable combination	AIC
James et al. (2015) – NDVI	75,055.03
+ annual temperature range	75,014.42
+ temperature seasonality, + annual temperature range	74,958.20
+ precipitation of driest month	74,912.35
+ temperature seasonality	74,890.93
+ temperature seasonality, + precipitation of driest month	74,847.95
+ annual temperature range, + precipitation of driest month	74,846.14
+ temperature seasonality, + annual temperature range, + precipitation of driest month ^a	74,737.60

^a Indicates final set of environmental variables used for model development.

include bioclimatic variables that are considered unimportant to tick phenology or survival (Elith and Leathwick, 2009; James et al., 2015). Our starting point for environmental variable selection was the set of variables used by James et al. (2015), except for Normalized Difference Vegetation Index (NDVI) data. We did not include NDVI data because there is uncertainty about how vegetation and land-use patterns might change in the future at a continental scale (Lambin et al., 2000), and data are unavailable in a format usable for our Maxent model and climate change projections. To assess the spatial correlation between all pairs of environmental variables, we calculated Spearman's rank coefficients using ENMTools v1.4.3 (Warren et al., 2010; Warren and Seifert, 2011); variables that were correlated ($r > 0.7$) and of low biological relevance for explaining the distribution of *D. variabilis* were removed from the model without affecting the overall predictive ability (see description of model evaluation below).

In total, we evaluated eight different combinations of environmental variables using the model selection tool in ENMTools (Table 1). We selected the combination of variables that exhibited the lowest value of Akaike's Information Criterion (AIC) as the final set of environmental variables for the development of the species distribution model for *D. variabilis* (Elith and Leathwick, 2009; James et al., 2015) because it produced the most parsimonious and explanatory model (Burnham and Anderson, 2002).

2.3. Model development and evaluation

We developed the model using the default convergence threshold (10^5), maximum iterations (500), regularization multiplier ($\beta = 1$), and number of background points (10,000). To build the model, we used a random subset of 80% of the occurrence data; the remaining 20% was withheld from model development and used to test the predictive ability of the final model. This method is commonly used when spatially independent data are unavailable, although it can potentially result in a model that overestimates suitability compared to one developed and tested using spatially independent data (Bahn and McGill, 2013). We replicated the model 10 times using the cross-validation setting, which allowed groups of occurrence points to be used for both model development and evaluation to produce a robust model (Araújo et al., 2005; Elith and Leathwick, 2009). Maxent assigns a value between 0 and 1 to each grid cell to represent the probability of climate suitability, where a value closer to 1 suggests a higher probability of suitability for *D. variabilis*. A threshold is then used to select the probability value below which grid cells were classified as unsuitable, and above which grid cells were classified as suitable. James et al. (2015) used the *minimum*

training threshold method to produce their model. The minimum training threshold might theoretically be the most suitable threshold for a problem such as this one, where erring on the side of caution might be considered worse than overestimating the possible distribution. We tried the minimum training threshold method, but found that, when applied to the now enlarged set of presence observations (see above, § Tick occurrence data), the model strongly overestimated the occurrence range, suggesting that nearly all of North America had suitable climate. We then tried the *10th-percentile training threshold*. The 10th-percentile training threshold identifies the probability at which the suitable area encompasses 90% of the occurrence records, suggesting that it is a liberal threshold, but does not overestimate the species' distribution (Phillips and Dudík, 2008; Rödder et al., 2009). Using this threshold, we found a much more suitable fit to the observed data, and the resulting model passed the subsequent validation test. We used the probability value that maximized model sensitivity and specificity to classify suitable cells further as moderately suitable or highly suitable. To evaluate the predictive accuracy of the Maxent model for *D. variabilis*, we used the area under the curve of the receiver operating characteristic (AUC ROC), which quantifies the ability of the model to classify a location accurately as suitable or unsuitable (Elith et al., 2006; Franklin, 2009).

2.4. Climate change projections

Maxent estimates a species' distribution under future climate change by determining geographic areas that are likely to exhibit climate conditions similar to the conditions found at occurrence points under present climate (Phillips et al., 2006; Merow et al., 2013). We projected the distribution of *D. variabilis* under climate change using four emissions scenarios (Representative Concentration Pathways, RCPs) from the Intergovernmental Panel for Climate Change (IPCC), 10 climate models from the Coupled Model Intercomparison Project (phase 5; CMIP5), and two time periods (for a total of 80 projections). We downloaded climate change data for each scenario, model, and year from Worldclim with a resolution of 2.5 arc minutes and processed them to match the extent of the baseline environmental variables described previously.

Four emissions scenarios represent a range of possible future climates based on projected radiative forcing for the years 2050 (range 2041–2060) and 2070 (range 2061–2080). Representative Concentration Pathway 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 depict low, low-moderate, high-moderate, and high radiative forcing respectively, where the projected increase in global temperature rises with increasing forcing (Harris et al., 2014; IPCC, 2014). Based on data availability for environmental variables and emissions scenarios, we selected 10 climate models: BCC-CSM1, CCSM4, HadGEM2-AO, HadGEM2-ES, GISS-ER-2, IPSL-CM5A-LR, MIROC5, MIROC-ESM, MRI-CGCM3, and NorESM1-M.

We ran the species distribution model for *D. variabilis* under climate change for each year and scenario with each of the 10 climate models using the same settings described above. We then used ArcGIS to calculate the 10-model mean probability of climate suitability to produce a consensus map for each RCP and year combination, as well as a corresponding map of the coefficient of variation for each RCP and year combination. We then calculated the area of suitable climate for each consensus map. Using multiple climate models and emissions scenarios allowed us to produce a range of possible future distributions of *D. variabilis*, showing the potential minimum and maximum extents of distributional change (Harris et al., 2014). Calculating the coefficient of variation for each consensus map produced a visual representation of climate model uncertainty associated with these model projections.

Table 2

List of environmental variables used for model development and their contribution to the model.

Variable name	Definition	Contribution (%)
bio05	Maximum temperature of warmest month	61.2
altitude	Meters above sea level	9.7
bio14	Precipitation of driest month	7.2
bio06	Minimum temperature of coldest month	7.1
bio13	Precipitation of wettest month	6.1
bio04	Temperature seasonality (standard deviation, mean annual temperature)	3.4
bio15	Precipitation seasonality (coefficient of variation)	2.1
bio07	Annual temperature range	1.7
bio03	Isothermality	1.1
bio02	Mean diurnal temperature range	0.4

3. Results

3.1. Environmental variable selection

In total, we used 10 environmental variables to develop the species distribution model for *D. variabilis* (Table 2). The combination of environmental variables that exhibited the lowest AIC value included all variables selected by James et al. (2015) (excluding July NDVI) plus temperature seasonality, annual temperature range, and precipitation of the driest month (Table 1). We included temperature seasonality and annual temperature range because of the importance of temperature ranges and extremes for survival and development of the immature stages of *D. variabilis* (Monello and Gompper, 2007; Atkinson et al., 2012). We note that mean temperature, while not included in our models, was highly correlated with several other climate variables, and was not included for this reason. Also, we thought it important to identify areas where climate extremes, rather than climate means, might affect the tick's range. James et al. (2015) used NDVI as a proxy variable for humidity. Since NDVI is not readily available for future climates, we could not use this variable. Instead, we included precipitation of the driest month to represent the high humidity and moisture availability requirements of *D. variabilis* and its susceptibility to desiccation off-host (Wimberly et al., 2008).

In the final species distribution model for *D. variabilis*, one variable contributed most of the environmental information (61.2%): maximum temperature of the warmest month. The maximum contribution of any other variable was 9.7%, represented by altitude (Table 2). Two variables, isothermality and mean diurnal temperature range, made minimal contributions to the model relative to the other variables based on percent contribution; however, jackknife results suggest that the gain and AUC (i.e. predictive ability) of the model is greater when these variables are included in the model compared to when they are excluded.

3.2. Model evaluation

The model predicted the climate to be suitable (probability of climate suitability > 0.276) where *D. variabilis* has been recorded throughout the eastern United States, the West Coast of the United States, southern Canada, and the Gulf Coast of Mexico, compared to regions where *D. variabilis* occurrences were not recorded (Fig. 1a vs. Fig. 1b). The mean test AUC ROC (0.865 ± 0.007) was greater than 0.5, which indicates that the model makes predictions with better accuracy than by random chance. It was also greater than 0.7, which indicates that the model accurately predicts a high probability of suitability in climatically suitable areas and low probability of suitability in climatically unsuitable areas (Fielding and Bell, 1997). Overall, based on visual representation and AUC ROC values, the final model accurately estimated the current distribution of *D. variabilis* in North

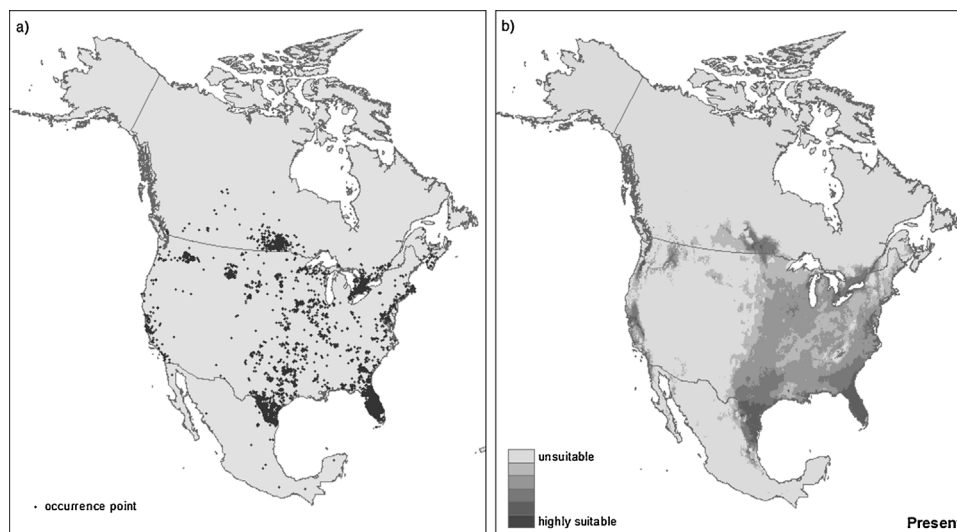


Fig. 1. (a) Map of *D. variabilis* occurrence records used for model development ($n = 3063$) and (b) map of current distribution of suitable climate for *D. variabilis* in North America.

America.

3.3. Climate change projections

Under all emissions scenarios, the mean of the 10 models indicated an overall increase in area of suitable climate from present, and a greater increase in moderately suitable area relative to highly suitable area, which decreases (Fig. 2). By 2050, the overall land area with suitable climate for *D. variabilis* is projected to increase by 30–42% from present, and by 2070 the area of suitable climate could increase by 31–53% from present, depending on which emissions trajectory was used. Representative Concentration Pathway 8.5 (year 2070) projected the greatest increase in suitable climate area from present and RCP 2.6 (year 2050) projected the least change in suitable climate area from present (Fig. 3).

Throughout the northern range of *D. variabilis*, all emissions scenarios projected a potential increase in climate suitability by 2050 and 2070. All scenarios projected an expansion of climatically suitable area toward the northwest in Canada, although the extent of this change was minor under lower emissions scenarios (e.g. Fig. 3a) and greater under higher emissions scenarios (e.g. Fig. 3c). The northernmost regions of the Prairies (i.e. Alberta, Saskatchewan, and Manitoba) and Ontario are projected to remain unsuitable under RCP 2.6, RCP 4.5, and RCP 6.0

(Figs. S1–S6); however, these areas are projected to become suitable under RCP 8.5, along with eastern British Columbia and southern Yukon Territory. In eastern Canada, the Maritime provinces are projected to become increasingly suitable for *D. variabilis* over time and with increasing emissions (Figs. S1–S6), and a larger portion of southern Quebec is projected to become suitable under RCP 8.5 (Fig. 3c).

The distribution of suitable climate in the southern range of *D. variabilis* is projected to remain relatively similar through 2050 and 2070, with the exception of parts of the southeastern United States and Mexico. Climate is projected to remain suitable throughout the eastern half of the United States under RCP 2.6, RCP 4.5, and RCP 6.0; however, it is likely that climate in the northeastern states, southeastern states, and the Gulf Coast of Mexico will be less suitable for *D. variabilis* than under present conditions (Fig. 2 vs. Fig. 3c). Under RCP 8.5, Mexico is projected to become unsuitable for *D. variabilis*, along with parts of some southeastern states: northeastern Texas, Arkansas, eastern Tennessee, western North Carolina, and northern Alabama and Georgia (Fig. 3c).

Based on the coefficient of variation of the model projections, all climate models were in good agreement on where the climate will be suitable for *D. variabilis* under all emissions scenarios in 2050 and 2070. Regions that the models agreed will likely have suitable climate for *D.*

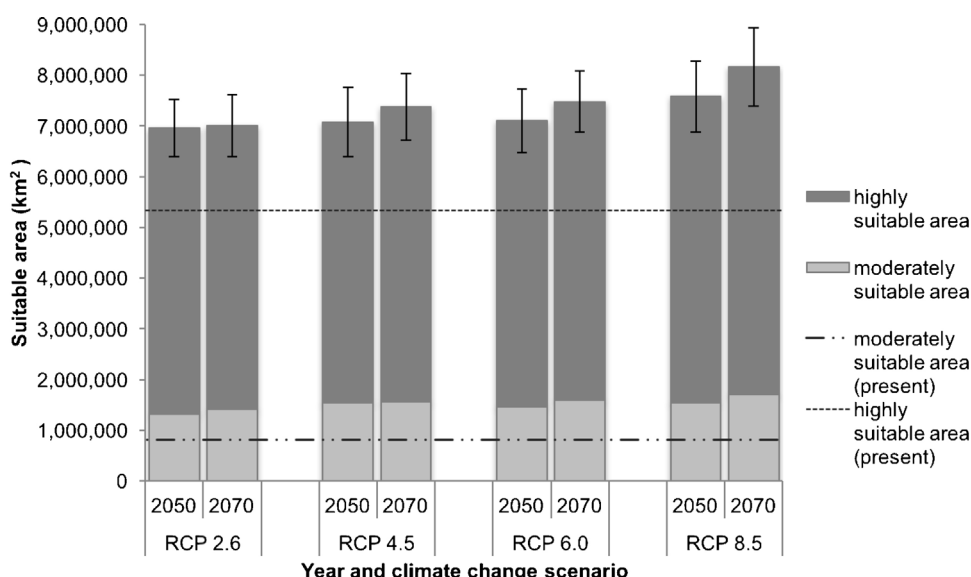


Fig. 2. Area of moderately and highly suitable climate for *D. variabilis* estimated by four climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) in years 2050 and 2070. Horizontal lines indicate the area of moderately and highly suitable climate for *D. variabilis* under baseline climate in North America.

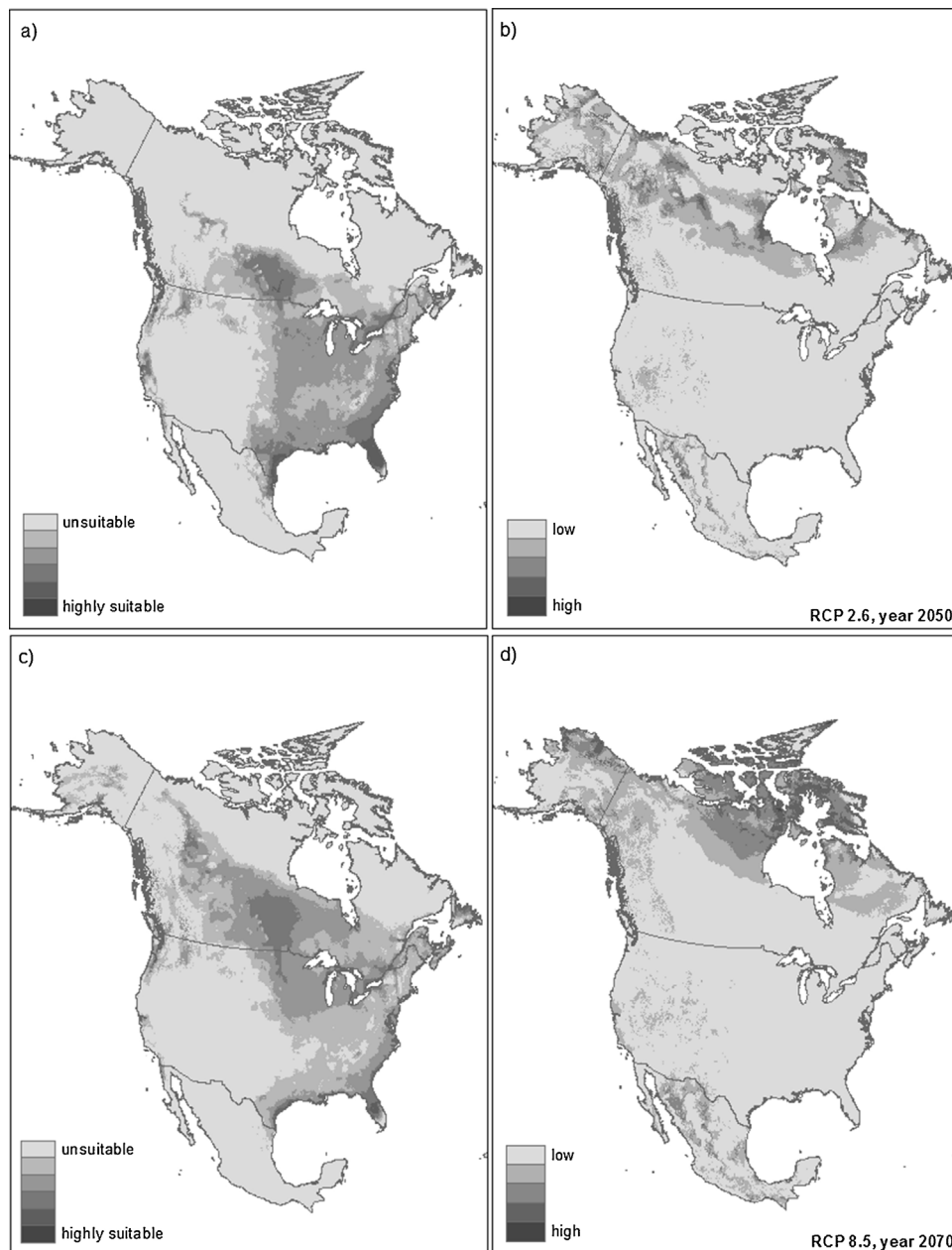


Fig. 3. (a) Potential climate suitability for *D. variabilis* under RCP 2.6, year 2050, (b) coefficient of variation of model agreement for RCP 2.6, year 2050, (c) potential climate suitability under RCP 8.5, year 2070, and (d) coefficient of variation of model agreement for RCP 8.5, year 2070.

variabilis in the future mainly encompassed areas that are currently suitable for the tick and which corresponded with the occurrence points. All climate models also agreed that the climate in the mountainous areas of western Canada and the eastern United States would not be suitable for *D. variabilis*. There was also disagreement among climate models regarding other areas where climate will likely be unsuitable, such as regions of northern Canada and arid regions of the western United States and Mexico. Each climate model makes different assumptions about which mechanisms to include, which to exclude, and which to incorporate phenomenologically, accounting for some disagreement about future climate suitability (IPCC, 2014; Newman et al., 2011). Disagreement and uncertainty about future climate suitability may be greater in extreme climates (e.g. deserts) or climates that are not well understood (e.g. the Arctic) (Knutti and Sedlek, 2012; IPCC, 2014).

4. Discussion

Tick distributions are limited by climate, host, and habitat

availability. Climate is a necessary but not sufficient condition for determining where *D. variabilis* is likely able to establish and thrive, notwithstanding any dispersal barriers (Süss et al., 2008). The effects of climate on *D. variabilis* individuals and populations are both direct and indirect; climate directly affects survival and development of *D. variabilis* individuals, and it indirectly affects populations of *D. variabilis* through its influence on host survival and habitat quality (Jongejan and Uilenberg, 2004). So, as a first approximation, we examined climate suitability for projecting the potential future distribution of *D. variabilis* under climate change (Walther et al., 2002; Pearson and Dawson, 2003), at a continental scale (Estrada-Peña et al., 2013). Further work combining habitat and/or host species distributions with the climate suitability shown here would be a valuable extension, but is beyond the scope of the present work (see e.g. Berzitis et al., 2014).

Based on climate only, our Maxent model predicted the known current distribution of *D. variabilis* well, indicating suitable climate across the eastern half of the United States and Canada and the Gulf Coast of Mexico, consistent with the North American distribution described in the literature (Sonenshine, 1993; Pfäffle et al., 2013) and the

distribution in the United States modeled by James et al. (2015). Our model and James et al. (2015) predicted high climate suitability in Florida and along the East Coast, as well as patches of unsuitable climate in the Midwest and northeastern United States. The climate in the Midwest and along the shores of the Great Lakes was predicted to be suitable by both models, but it was more suitable in predictions by James et al. (2015) than by our model. Both models predicted suitable climate along the West Coast of the United States; however, James et al. (2015) predicted relatively high suitability in the northwestern states compared to our model results, which predicted climate in this region to be mostly unsuitable for *D. variabilis*.

The differences between the results of our model and the results of James et al. (2015) are likely due to our inclusion of Canadian and Mexican occurrence data. Maxent identifies the average climate conditions at the occurrence points (i.e. suitable climate conditions) and locates other grid cells that exhibit similar average conditions (Phillips et al., 2006; Elith et al., 2011). Because we developed our model using a larger set of occurrence points, from a larger geographic space, with a wider range of climate conditions than other models of the distribution of *D. variabilis* (all of North America vs. United States only), the specific set of climate conditions that Maxent considered suitable for *D. variabilis* is likely different in our model than previous models.

We also developed our model using a slightly different set of environmental variables than that of James et al. (2015) to represent the climate requirements of *D. variabilis* that could be projected under potential future conditions. The inclusion of additional variables and the resulting percent contribution of each variable likely influenced the average suitable climate conditions at the occurrence points (Elith et al., 2011), contributing to the differences in the current distribution of suitable climate between our model and the model by James et al. (2015). Despite the differences in variable selection, both models considered maximum temperature of the warmest month and altitude to be the most important variables based on percent contribution, although our model considered altitude to be less important than the maximum temperature of the warmest month and it contributed less to our model compared to the model by James et al. (2015).

Minimum precipitation of the driest month and minimum temperature of the coldest month were important variables in the final species distribution model for *D. variabilis*, in addition to maximum temperature of the warmest month. Under climate change, minimum and maximum temperatures are expected to rise continually across much of North America over the course of the current century (IPCC, 2014), which could potentially result in the northward expansion of the range of *D. variabilis* in northern Ontario and the Prairies that our model projected. Development of immature stages of *D. variabilis* is temperature dependent, especially throughout the northernmost range of the tick, and it is possible that winter temperatures in the northeastern United States and southern Canada limit the northern distribution of *D. variabilis*. In the absence of protective habitat, temperatures below the cold threshold of *D. variabilis* can reduce overwintering survival of ticks. Temperatures that are too low (or too high) can also slow or prevent egg development and transitions from one life stage to the next in any season (Sonenshine, 1991). Under climate change, a rise in winter temperatures could improve overwintering and egg survival, improving overall population success for *D. variabilis* (Sonenshine, 1993; Pfäffle et al., 2013). Additionally, locations that are currently too cold for *D. variabilis* to establish could become warm enough to support tick species (Porretta et al., 2013), as might already be the case for *I. scapularis* in southern Canada (Ogden et al., 2006). Warmer, shorter winters also promote a longer active season for *D. variabilis* and its hosts, which likely increases the frequency of tick-host encounters and the resulting disease incidence (Estrada-Peña, 2008).

Increasing maximum temperatures can influence the rate of evaporation and, in combination with changing precipitation patterns, the overall moisture availability within tick habitat (IPCC, 2014). Moisture availability is important for egg and immature tick development, and is

crucial for off-host survival of *D. variabilis* individuals where they reside in the microclimate, exposed to extreme weather conditions and susceptible to desiccation in dry conditions (Sonenshine, 1991, 1993). It is possible that the environment will no longer support *D. variabilis* populations where dry conditions are likely to occur under climate change, such as the southern United States and parts of Mexico, where our model projected unsuitable climate for *D. variabilis* under higher emissions scenarios.

All else being equal, active surveillance data should be the gold standard for any tick distribution model (see e.g. Simon et al., 2014). Our species distribution model for *D. variabilis* was developed primarily using passive surveillance data collected by the public and researchers, as were other species distribution models that have been developed for ticks (e.g. James et al., 2006; Atkinson et al., 2012; Porretta et al., 2013). The data represent ticks found on humans, pets, and wildlife that were submitted to, and identified by, experts at museums and laboratories across North America. It is not uncommon to use passive surveillance data in medical entomology, and as presence-only data in species distribution models, because they allow researchers to gather data over a long period of time or from a large geographic area (Nelder et al., 2014; Pacifici et al., 2017) without encountering some of the disadvantages of active surveillance, such as personnel time and financial costs (Rand et al., 2007; Leighton et al., 2012). Of course, a disadvantage of passive surveillance data is the assumption that all ticks originate from the location at which they were found (i.e. were not adventitious). Here, it is likely that a portion of the records used to develop the species distribution model correspond with adventitious ticks; however, we developed our model using a large number of occurrence points across North America, often with multiple records per county or Forward Sortation Area. In this case, we thought it unlikely that the number of (unknown) potentially spurious records produced significant bias in the overall results of the model (Wisz et al., 2008), so we did not assume that specific records corresponded with adventitious ticks and thus retained all records throughout the model development process. Additionally, use of the 10th-percentile training threshold for binary classification excludes the locations with suitable climate associated with 10% of occurrence records that have the most extreme climate conditions relative to the majority of records (Phillips and Dudík, 2008). These eliminated occurrence points would likely include spurious records from adventitious ticks found outside their native suitable climate areas.

Tick species distribution models would be greatly improved if active surveillance data were more readily available, and available for much larger geographic areas. Notwithstanding this, species distribution models provide reasonably reliable representations of current and potential future distributions of species, despite the potential issues associated with passive surveillance data and additional limitations of archived presence-only data (Elith and Leathwick, 2009); however, the quality of the results is dependent on the input data, and results should be interpreted with caution, especially when modeling species like ticks, which can be difficult to detect or can be transported by a host. Species distribution models often describe a species' distribution based only on abiotic conditions, such as climate, and are unable to include biotic components in detail (Pearson and Dawson, 2003), including interactions with other species (but see, e.g. Berzitis et al., 2014) such as vertebrate hosts. For *D. variabilis* and other ticks, a complete assessment of the risk of pathogen transmission requires information on current and projected future locations of the tick combined with information on areas where the climate will potentially be suitable for host and pathogen success. This is especially important in regions where *D. variabilis* occurs, where tick-borne pathogen transmission could increase in the future based on a potential increase in climate suitability for the tick vector, and subsequent changing tick exposure due to increased tick-host encounters.

Acknowledgments

The authors thank Dr. Lorenza Beati and Colleen Evans of the United States National Tick Collection, Dr. Jack Schlater of the National Veterinary Services Laboratory, Dr. Donald Martin of IDEXX Laboratories, and Dr. Terry Galloway of the Wallis-Roughley Museum of Entomology for providing tick occurrence data. The authors also thank Alison Moore and Dr. Amy Greer for helpful discussion, Dr. Neftal Sillero for modeling guidance, and the staff at the Data Resource Centre of the University of Guelph for GIS assistance. JNM was supported by a scholarship from the Ontario Ministry of Agriculture, Food and Rural Affairs. The research was supported by a grant from the Canadian Natural Science and Engineering Research Council to JAN, and a grant from the Ontario Ministry of Agriculture, Food and Rural Affairs to JAN, HAH, and AP.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ttbdis.2017.11.012>.

References

- Araújo, M.B., Pearson, R.G., 2005. Equilibrium of species' distributions with climate. *Ecography* 28, 693–695.
- Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. *Glob. Change Biol.* 11, 1504–1513.
- Atkinson, S.F., Sarkar, S., Avia, A., Schuermann, J.A., Williamson, P., 2012. Modelling spatial concordance between Rocky Mountain spotted fever disease incidence and habitat probability of its vector *Dermacentor variabilis* (American dog tick). *Geospatial Health* 7, 91–100.
- Aubry, P., Geale, D.W., 2011. A review of bovine anaplasmosis. *Transbound. Emerg. Dis.* 58, 1–30.
- Bahn, V., McGill, B.J., 2013. Testing the predictive performance of distribution models. *Oikos* 122, 321–331.
- Berzitis, E.A., Minigan, J.N., Hallett, R.H., Newman, J.A., 2014. Climate and host plant availability impact the future distribution of the bean leaf beetle (*Ceratomyza trifurcata*). *Glob. Change Biol.* 20, 2778–2792.
- Bishopp, F.C., Trembley, H.L., 1945. Distribution and hosts of certain North American ticks. *J. Parasitol.* 31, 1–54.
- Bouchard, C., Leonard, E., Koffi, J.K., Pelcat, Y., Peregrine, A., Chinton, N., Rochon, K., Lysyk, T., Lindsay, L.R., Ogden, N.H., 2015. The increasing risk of Lyme disease in Canada. *Can. Vet. J.* 56, 693–699.
- Brownstein, J.S., Holford, T.R., Fish, D., 2005. Effect of climate change on Lyme disease risk in North America. *EcoHealth* 2, 38–46.
- Burg, J.G., 2001. Seasonal activity and spatial distribution of host-seeking adults of the tick *Dermacentor variabilis*. *Med. Vet. Entomol.* 15, 413–421.
- Burnham, K., Anderson, D., 2002. *Model Selection and Inference: A Practical Information Theoretic Approach*, 2nd ed. Springer.
- Dergousoff, S.J., Galloway, T.D., Lindsay, R., Curry, P.S., Chilton, N.B., 2013. Range expansion of *Dermacentor variabilis* and *Dermacentor andersoni* (Acari: Ixodidae) near their northern distributional limits. *J. Med. Entomol.* 50, 510–520.
- Dodds, D.G., Martell, A.M., Yescott, R.E., 1969. Ecology of the American dog tick, *Dermacentor variabilis* (Say), in Nova Scotia. *Can. J. Zool.* 47, 171–181.
- Eisen, L., Eisen, R.J., Lane, R.S., 2006. Geographical distribution patterns and habitat suitability models for presence of host-seeking ixodid ticks in dense woodlands of Mendocino County, California. *J. Med. Entomol.* 43, 415–427.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–697.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57.
- ESRI, 2014. *ArcGIS 10.3*. Environmental Systems Research Institute, Redlands, CA.
- Estrada-Peña, A., 2008. Climate, niche, ticks, and models: what they are and how we should interpret them. *Parasitol. Res.* 103, 87–95.
- Estrada-Peña, A., Estrada-Sánchez, A., Estrada-Sánchez, D., de la Fuente, J., 2013. Assessing the effects of variables and background selection on the capture of the tick climate niche. *Int. J. Health Geogr.* 1, 2. <http://dx.doi.org/10.1186/1476-072X-12-43>.
- Fayer, R., 2000. Global change and emerging infectious diseases. *J. Parasitol.* 86, 1174–1181.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Franklin, J., 2009. *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press, Cambridge, UK.
- Gage, K.L., Burkot, T.R., Eisen, R.J., Hayes, E.B., 2008. Climate and vectorborne diseases. *Am. J. Prev. Med.* 35, 436–450.
- Google. (n.d.) [Google Maps directions for driving from Ingolstadt, Germany, to Geneva, Switzerland]. Retrieved August 4, 2015, from <https://www.google.com/maps/>.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.
- Guzmán-Cornejo, C., Robbins, R.G., Guglielmo, A.A., Montiel-Parra, G., Rivas, G., Pérez, T.M., 2016. The *Dermacentor* (Acari, Ixodida, Ixodidae) of Mexico: hosts, geographical distribution and new records. *ZooKeys* 569, 1–22.
- Harris, R.M.B., Grose, M.R., Lee, G., Bindoff, N.L., Porfiro, L.L., Fox-Hughes, P., 2014. Climate projections for ecologists. *WIREs Clim. Change* 5, 621–637.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Howden, K.J., Geale, D.W., Par, J., Golsteyn-Thomas, E.J., Gajadhar, A.A., 2010. An update on bovine anaplasmosis (*Anaplasma marginale*) in Canada. *Can. Vet. J.* 51, 837–840.
- IPCC, 2014. In: Core Writing Team, R.K., Pachauri, L.A., Meyer (Eds.), *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland 151 pp.
- James, A.M., Freier, J.E., Keirans, J.E., Durden, L.A., Mertins, J.W., Schalter, J.L., 2006. Distribution, seasonality, and hosts of the Rocky Mountain wood tick in the United States. *J. Med. Entomol.* 43, 17–24.
- James, A.M., Burdett, C., McCool, M.J., Fox, A., Riggs, P., 2015. The geographic distribution and ecological preferences of the American dog tick, *Dermacentor variabilis* (Say), in the U.S.A. *Med. Vet. Entomol.* 29, 178–188.
- Jongejan, F., Uilenberg, G., 2004. The global importance of ticks. *Parasitology* 129, S3–S14.
- Knutti, R., Sedleir, J., 2012. Robustness and uncertainties in the new CMIP5 climate model projections. *Nat. Clim. Change* 3, 369–373.
- Kocan, K.M., de la Fuente, J., Blouin, E.F., Coetzee, J.F., Ewing, S.A., 2010. The natural history of *Anaplasma marginale*. *Vet. Parasitol.* 167, 95–107.
- Lambin, E.F., Rounsevell, M.D.A., Geist, H.J., 2000. Are agricultural land-use models able to predict changes in land-use intensity? *Agric. Ecosyst. Environ.* 82, 321–331.
- Léger, E., Vourc'h, G., Vial, L., Chevillon, C., McCoy, K.D., 2013. Changing distributions of ticks: causes and consequences. *Exp. Appl. Acarol.* 59, 219–244.
- Leighton, P.A., Koffi, J.K., Pelcat, Y., Lindsay, L.R., Ogden, N.H., 2012. Predicting the speed of tick invasion: an empirical model of range expansion for Lyme disease vector *Ixodes scapularis* in Canada. *J. Appl. Ecol.* 49, 457–464.
- Lindgren, E., Gustafson, R., 2001. Tick-borne encephalitis in Sweden and climate change. *Lancet* 358, 16–18.
- Lindquist, E., Galloway, T., Artsob, H., Lindsay, R., Drebot, M., Wood, H., Robbins, R., 2016. *A Handbook to the Ticks (Ixodida: Ixodidae, Argasidae) of Canada*, 1st ed. *Biological Survey of Canada*. <http://dx.doi.org/10.3752/9780968932186>.
- Lysyk, T.J., 2013. Movement of male *Dermacentor andersoni* (Acari: Ixodidae) among cattle. *J. Med. Entomol.* 50, 977–985.
- Martinez-Meyer, E., 2005. Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodivers. Inform.* 2, 42–55.
- Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069.
- Minigan, J.N., Hager, H.A., Peregrine, A.S., Newman, J.A., 2015. Current and Potential Future Distribution of the American Dog Tick (*Dermacentor variabilis*, Say) in North America. *Agri-Environmental Research Data Repository*, University of Guelph. <http://bit.ly/2x5vdbn>.
- Monello, R.J., Gompert, M.E., 2007. Biotic and abiotic predictors of tick (*Dermacentor variabilis*) abundance and engorgement on free-ranging raccoons (*Procyon lotor*). *Parasitology* 134, 2053–2062.
- Nelder, M.P., Russell, C., Lindsay, R.L., Dhar, B., Patel, S.N., Johnson, S., Moore, S., Kristjansson, E., Li, Y., Ralevski, F., 2014. Population-based passive tick surveillance and detection of expanding foci of blacklegged ticks *Ixodes scapularis* and the Lyme disease agent *Borrelia burgdorferi* in Ontario, Canada. *PLOS ONE* 9, e105358.
- Newman, J.A., Anand, M., Henry, H.A.L., Hunt, S., Gedalof, Z., 2011. *Climate Change Biology*. CAB International.
- Ogden, N.H., Trudel, L., Artsob, H., Barker, I.K., Beauchamp, G., Charron, D.F., Drebot, M.A., Galloway, T.D., O'Handley, R., Thompson, R.A., Lindsay, L.R., 2006. *Ixodes scapularis* ticks collected by passive surveillance in Canada: analysis of geographic distribution and infection with Lyme Borrelia agent *Borrelia burgdorferi*. *J. Med. Entomol.* 43, 600–609.
- Ogden, N.H., St-Onge, L., Barker, I.K., Brazeau, S., Bigras-Poulin, M., Charron, D.F., Francis, C.M., Heagy, A., Lindsay, R., Maarouf, A., Michel, P., Milord, F., O'Callaghan, C.J., Trudel, L., Thompson, A., 2008. Risk maps for range expansion of the Lyme disease vector, *Ixodes scapularis*, in Canada now and with climate change. *Int. J. Health Geogr.* 7. <http://dx.doi.org/10.1186/1476-072X-7-24>.
- Pacifici, K., Reich, B.J., Miller, D.A.W., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., Collazo, J.A., 2017. Integrating multiple data sources in species distribution modeling: a framework for data fusion. *Ecology* 98, 840–850.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
- Pfäffle, M., Littwin, N., Maders, S.V., Petney, T.N., 2013. The ecology of tick-borne diseases. *Int. J. Parasitol.* 43, 1059–1077.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.

- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Porretta, D., Mastrantonio, V., Amendolia, S., Gaiarsa, S., Epis, S., Genchi, C., Bandi, C., Otranto, D., Urbanelli, S., 2013. Effects of global changes on the climatic niche of the tick *Ixodes ricinus* inferred by species distribution modelling. *Parasite Vector* 6, 271–278.
- Porter, W.P., Kearney, M., 2009. Size, shape, and the thermal niche of endotherms. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19666–19672.
- Rand, P.W., Lacombe, E.H., Dearborn, R., Cahill, B., Elias, S., Lubelczyk, C.B., Beckett, G.A., Smith Jr., R.P., 2007. Passive surveillance in Maine, an area emergent for tick-borne diseases. *J. Med. Entomol.* 44, 1118–1129.
- Rödger, D., Kielgast, J., Bielby, J., Schmidtlein, S., Bosch, J., Garner, T.W.J., Veith, M., Walker, S., Fisher, M.C., Lters, S., 2009. Global amphibian extinction risk assessment for the panzootic chytrid fungus. *Diversity* 1, 52–66.
- Simon, J.A., Marrotte, R.R., Desrosiers, N., Fiset, J., Gaitan, J., Gonzalez, A., Koffi, J.K., Lapointe, F.J., Leighton, P.A., Lindsay, L.R., Logan, T., 2014. Climate change and habitat fragmentation drive the occurrence of *Borrelia burgdorferi*, the agent of Lyme disease, at the northeastern limit of its distribution. *Evol. Appl.* 7, 750–764.
- Sonenshine, D.E., 1991. *Biology of Ticks*, vol. 1 Oxford University Press, New York.
- Sonenshine, D.E., 1993. *Biology of Ticks*, vol. 2 Oxford University Press, New York.
- St. John, H.K., Adams, M.L., Masuoka, P.M., Flyer-Adams, J.G., Jiang, J., Rozmajzl, P.J., Stromdahl, E.Y., Richards, A.L., 2016. Prevalence, distribution, and development of an ecological niche model of *Dermacentor variabilis* ticks positive for *Rickettsia montanensis*. *Vector Borne Zoonotic Dis.* 16, 253–263.
- Süss, J., Klaus, C., Gerstengarbe, F., Werner, P.C., 2008. What makes ticks tick? Climate change, ticks, and tick-borne diseases. *J. Travel Med.* 15, 39–45.
- Thomas, S.M., Beierkuhnlein, C., 2013. Predicting ectotherm disease vector spread-benefits from multidisciplinary approaches and directions forward. *Naturwissenschaften* 100, 395–405.
- Troughton, D.R., Levin, M.L., 2007. Life cycles of seven ixodid tick species (Acari: Ixodidae) under standardized laboratory conditions. *J. Med. Entomol.* 44, 732–740.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342.
- Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33, 607–611.
- Wimberly, M.C., Yabsley, M.J., Baer, A.D., Dugan, V.G., Davidson, W.R., 2008. Spatial heterogeneity of climate and land-cover constraints on distributions of tick-borne pathogens. *Glob. Ecol. Biogeogr.* 17, 189–202.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14, 763–773.